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MORPHOLOGY OF THE MALE INTERNAL REPRODUCTIVE SYSTEM IN ARMY ANTS: PHYLOGENETIC IMPLICATIONS (HYMENOPTERA: FORMICIDAE)

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Abstract.—The morphology of the male internal reproductive system is described for representative species of New and Old World army ants. Functional testes in these species are present only in the pupa. The testes atrophy to such extent prior to or at the time of eclosion that little evidence of their existence in the adult can be found. Spermatogenesis and the storage of newly formed sperm cells in the seminal vesicles thus occur during pupal development before emergence. The internal genital structures are most derived and uniquely developed in New World species and least so in Old World species. The extraordinary differences in male internal genitalic morphology between New and Old World forms constitute further evidence of the polyphyletic origin of army ants.

The internal reproductive system of male ants includes a pair of testes, their vasa deferentia, and a pair of accessory glands. The vasa deferentia, ducts that connect the testes to the accessory glands, are expanded in some species to form seminal vesicles. The accessory glands empty through a pair of ducts that converge to form a common ejaculatory duct (Matsuda, 1976). This duct proceeds caudally where it enters the sclerotized genital capsule. Relatively few studies of these soft internal structures have been undertaken. Descriptions of this system in ants were published by Adlerz (1886), Janet (1902), Mukerjee (1926), Marcus (1953), Forbes (1954, 1958), Forbes and Do-Van-Quy (1965), Beck (1972), and Hung and Vinson (1975). Of these, only the studies of Mukerjee, Forbes (1958), Forbes and Do-Van-Quy, and Hung and Vinson deal specifically with or include army ants.

The "true" army ants were formerly placed in the single subfamily Dorylinae but are now regarded as two subfamilies. The New World genera (*Cheliomyrmex, Eciton, Labidus, Neivamyrmex,* and *Nomamyrmex*) are currently assembled in the subfamily Ecitoninae, while the Old World genera (*Aenictus* and *Dorylus*) comprise the Dorylinae (Snelling, in press). This reflects the generally held view that the doryline ants as previously consti-

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tuted are polyphyletic. Although Wheeler (1928) supposed that the dorylines shared a common ancestor, both Brown (1954) and Borgmeier (in Seevers, 1965) later hypothesized that the group was diphyletic. In studies of morphological, behavioral, and geographic characteristics, Gotwald (1969, 1977, 1979) and Gotwald and Kupiec (1975) speculated that the dorylines are triphyletic. They proposed that the New World dorylines constituted one lineage, the Old World genus *Dorylus* with its six subgenera (*Alaopone, Anomma, Dichthadia, Dorylus, Rhogmus,* and *Typhlopone*) a second, and the Old World genus *Aenictus* a third.

Most of the morphological and behavioral evidence upon which the polyphyletic hypothesis of doryline origins is based was gathered from the worker caste. The queens and males seem obvious candidates for similar evidence-gathering investigations. This is especially true for the males which possess a well-developed, conspicuous but retractile genital capsule. The sclerotized components of this capsule are commonly figured in taxonomic treatments of the army ants (see Borgmeier, 1955), but a comparative examination of the soft, internal reproductive structures of the males does not exist. Indeed, only one species of *Eciton* (Forbes, 1954), two of *Neivamyrmex* (Forbes and Do-Van-Quy, 1965; Hung and Vinson, 1975), and one of *Dorylus* (Mukerjee, 1926) have ever been described in the literature.[1]

The purpose of this paper is to describe the gross morphology and certain histological aspects of the male internal reproductive system in both Old and New World army ant species and to interpret the phylogenetic implications of this morphology. Special emphasis was placed on the subgenera of *Dorylus,* since one of us (WHG) is currently revising the Old World genera.

Methods and Terminology

Most specimens dissected were preserved in alcohol or Bouin's fluid although a few critical forms were available only as dried specimens. These were relaxed in 70% ethanol and then dissected. In a majority of the alcohol- or Bouin's-preserved specimens, the internal structures retained their elasticity to a remarkable degree. After being removed from the gaster, the reproductive structures were described and drawn. Specimens of all five New World genera and of both Old World genera, including all six subgenera of *Dorylus,* were dissected. Additionally, the male of one ponerine species was examined. Male pupae of the genera *Neivamyrmex* and *Dorylus* were also dissected.

The internal genitalia of two adult males of *Dorylus* (*Rhogmus*) were sectioned and stained with Delafield's hematoxylin-eosin. Also sectioned were the testes of a male pupa of *Dorylus* (*Anomma*). These sections were

[1] See Ford and Forbes, 1980, J. N.Y. Entomol. Soc. 83: 133–142 for an additional account of *Dorylus* male reproductive anatomy.

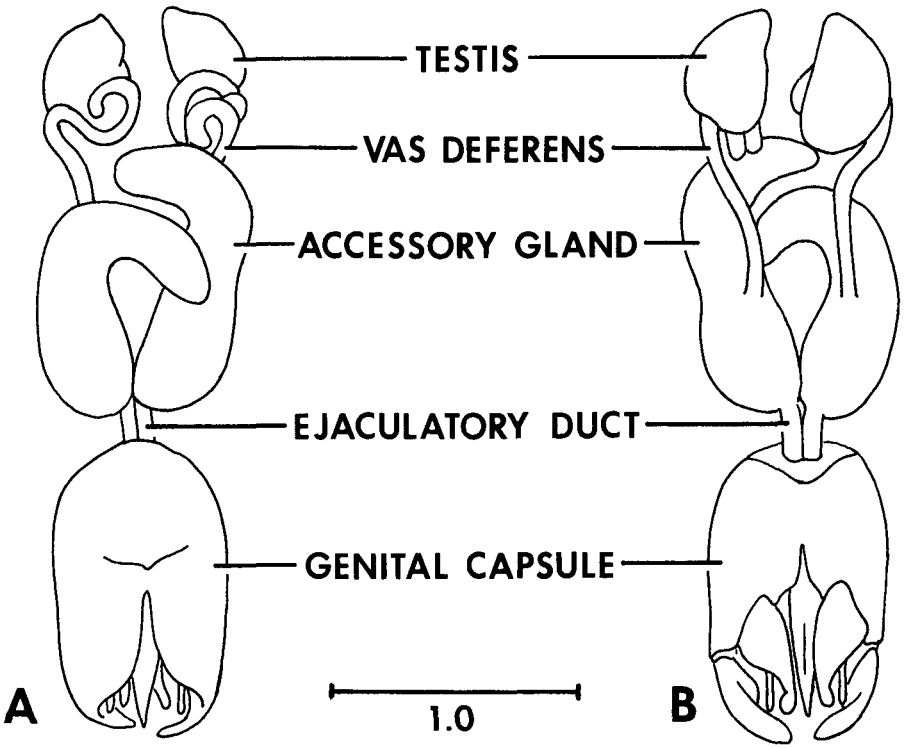

Fig. 1. Male reproductive system of *Plectroctena lygaria*. A, Dorsal view. B, Ventral view. Scale in mm.

stained with gallocyanin blue-phloxine. Serial sections of an entire adult male of *Labidus* were provided by Julian F. Watkins II.

Terms used for the male internal reproductive structures are essentially those of Snodgrass (1935) and Matsuda (1976). When functional, the testes are composed of a variable number of follicles in which spermatogenesis occurs. The vasa deferentia are the narrow tubes that transport the sperm cells from the testes to the middle or base of the accessory glands and/or ejaculatory duct. If the vasa deferentia are swollen and bulbous and function to store the spermatozoa, they are called the seminal vesicles. The accessory glands are usually dorsal to the vasa deferentia and probably contribute to the formation of seminal fluid. The ducts into which the accessory glands empty are here assumed to be the anterior, bifurcated ends of the ejaculatory duct. However, when these ducts unite to form the ejaculatory duct, their lumina usually remain separate and distinct. For this reason Forbes (1958) referred to the ejaculatory duct as the "bound accessory gland ducts." The term genital capsule is used to collectively denote the sclerotized external genitalia.

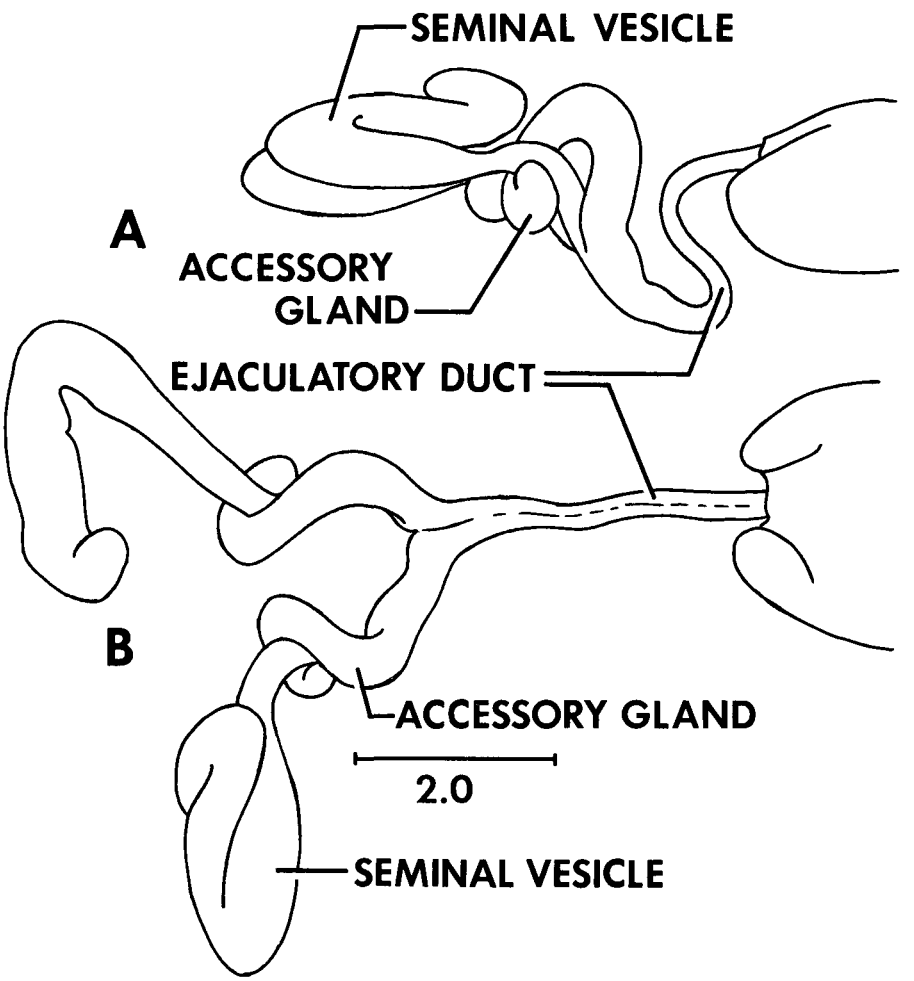

Fig. 2. Male reproductive system of *Cheliomyrmex morosus*. A, Lateral view. B, Dorsal view. Scale in mm.

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Subfamily Ponerinae

Plectroctena lygaria Bolton, Gotwald, and Leroux (1 specimen from the Laboratoire d'Ecologie Tropicale, Lamto, Ivory Coast) (Fig. 1).

Because the ponerines are among the most primitive or generalized of ants, a male of one ponerine, *P. lygaria,* was dissected to serve as a morphological "reference point." Each testis in this species is a conspicuous globular structure composed of sperm-producing follicles. Leading from

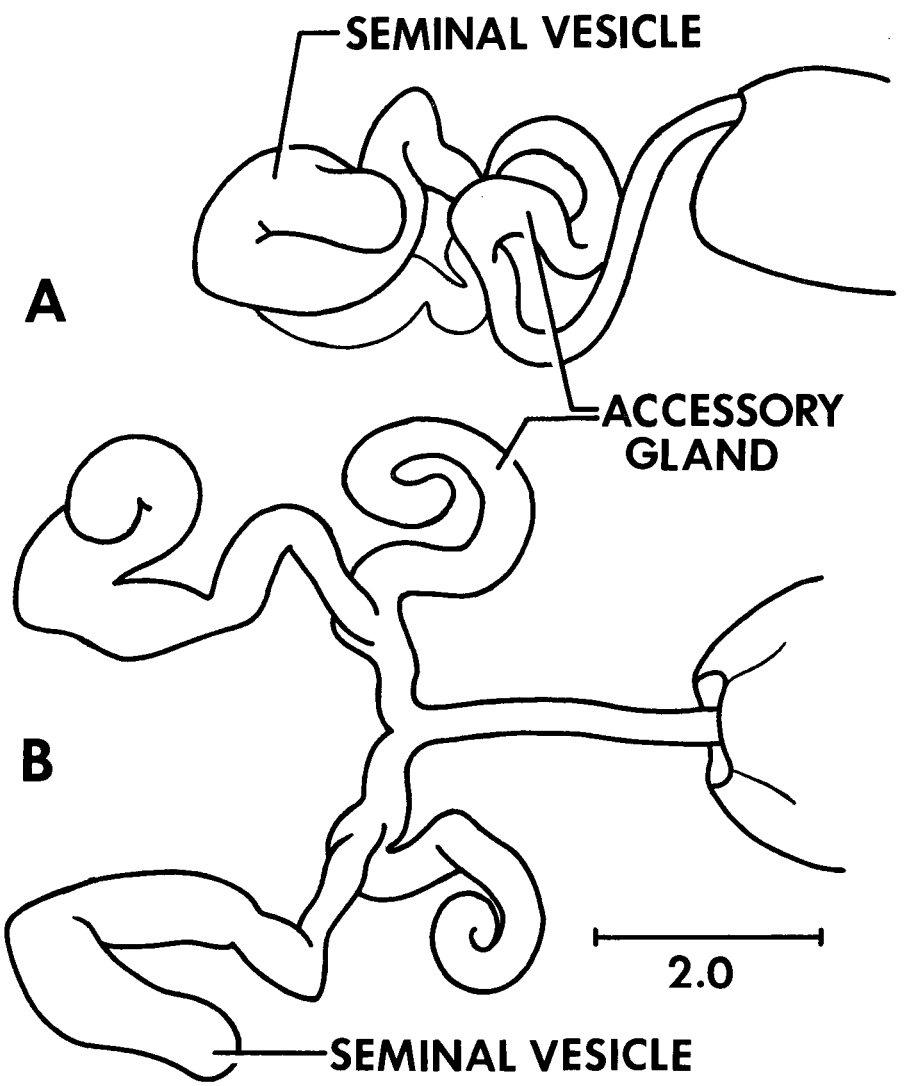
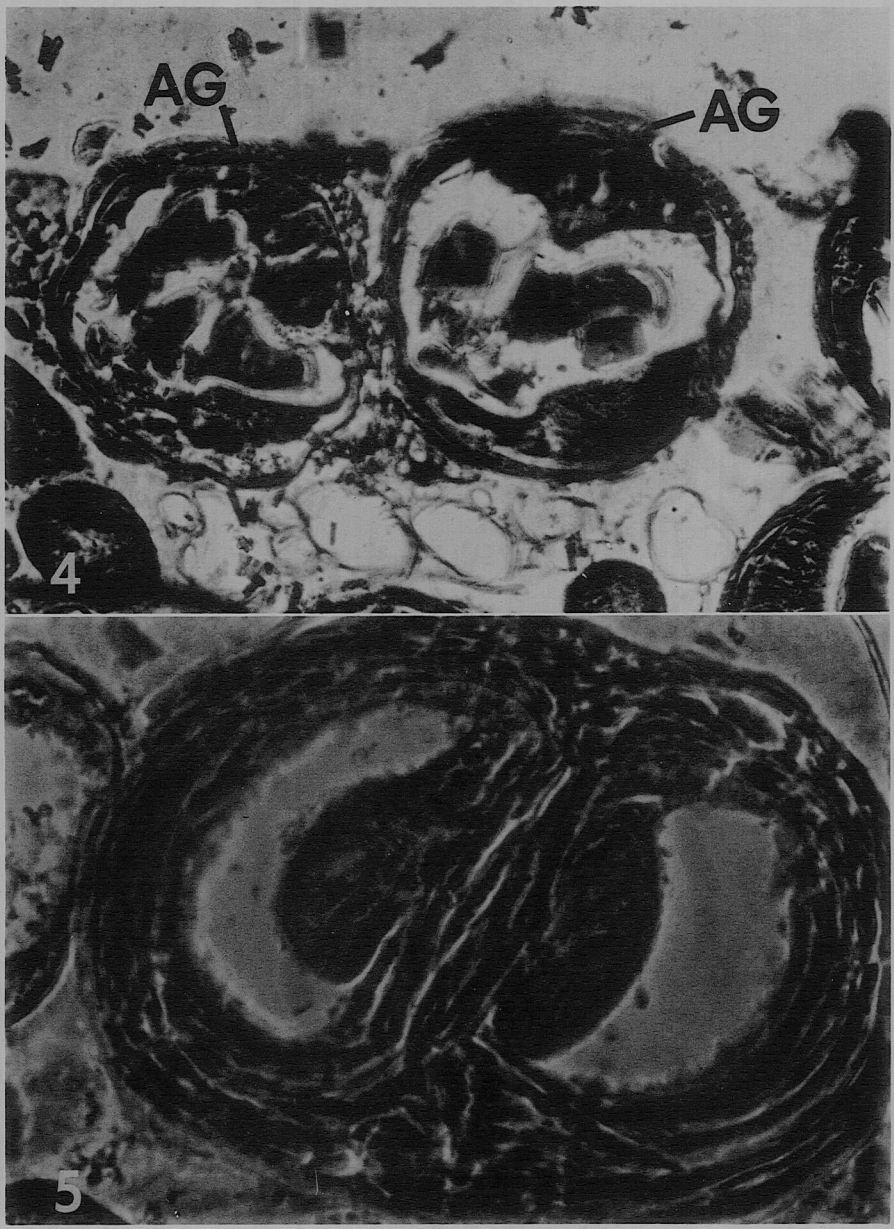


Fig. 3. Male reproductive system of *Labidus praedator*. A, Lateral view. B, Dorsal view, structures displaced for purpose of display. Scale in mm.

each testis is a narrow, distally convoluted vas deferens. This duct does not expand to form a seminal vesicle but instead continues without changing in diameter, attaching to the middle region of the ventral surface of the accessory gland. The two accessory glands are elongated, apically pointed bodies that are directed anteriorly. Although the ducts from the accessory glands



Figs. 4, 5. *Labidus coecus*, male. 4, Accessory gland, cross section; two sections can be seen (marked AG) (200×). 5, Ejaculatory duct, cross section (400×).

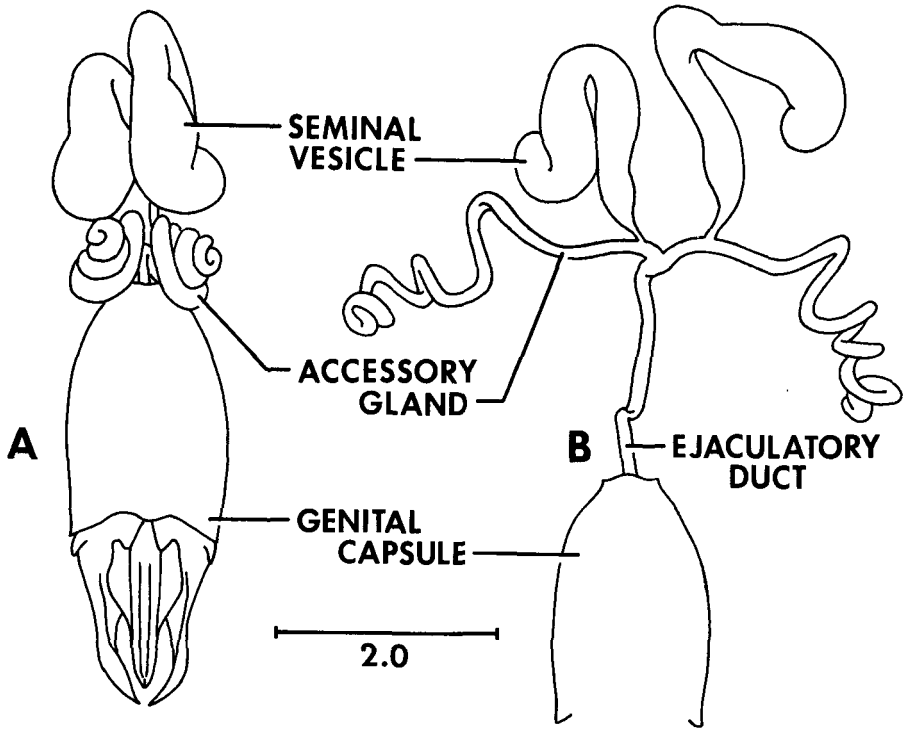


Fig. 6. Male reproductive system of *Neivamyrmex* sp. A, *In situ* dorsal view. B, Structures displaced for purpose of display, dorsal view. Scale in mm.

join to form a common ejaculatory duct, predictably their lumina are individually retained, even as the ejaculatory duct enters the genital capsule.

Subfamily Ecitoninae

Cheliomyrmex morosus (F. Smith) (1 specimen from Palenque, Mexico) (Fig. 2).

Testes are not evident. The seminal vesicles are elongated, sperm-filled sacs. Each is folded upon itself twice. The accessory glands are elongated structures, each of which is coiled once about the proximal end of its corresponding seminal vesicle. The ejaculatory duct forms a ventrally directed loop before entering the genital capsule.

Labidus praedator (F. Smith) (1 specimen from Tamazunchale, Mexico) (Fig. 3).

Testes are not evident. The seminal vesicles are elongated, folded sacs similar to those of *Cheliomyrmex*. Each opens into the proximal end of its corresponding accessory gland. The accessory glands are proportionately

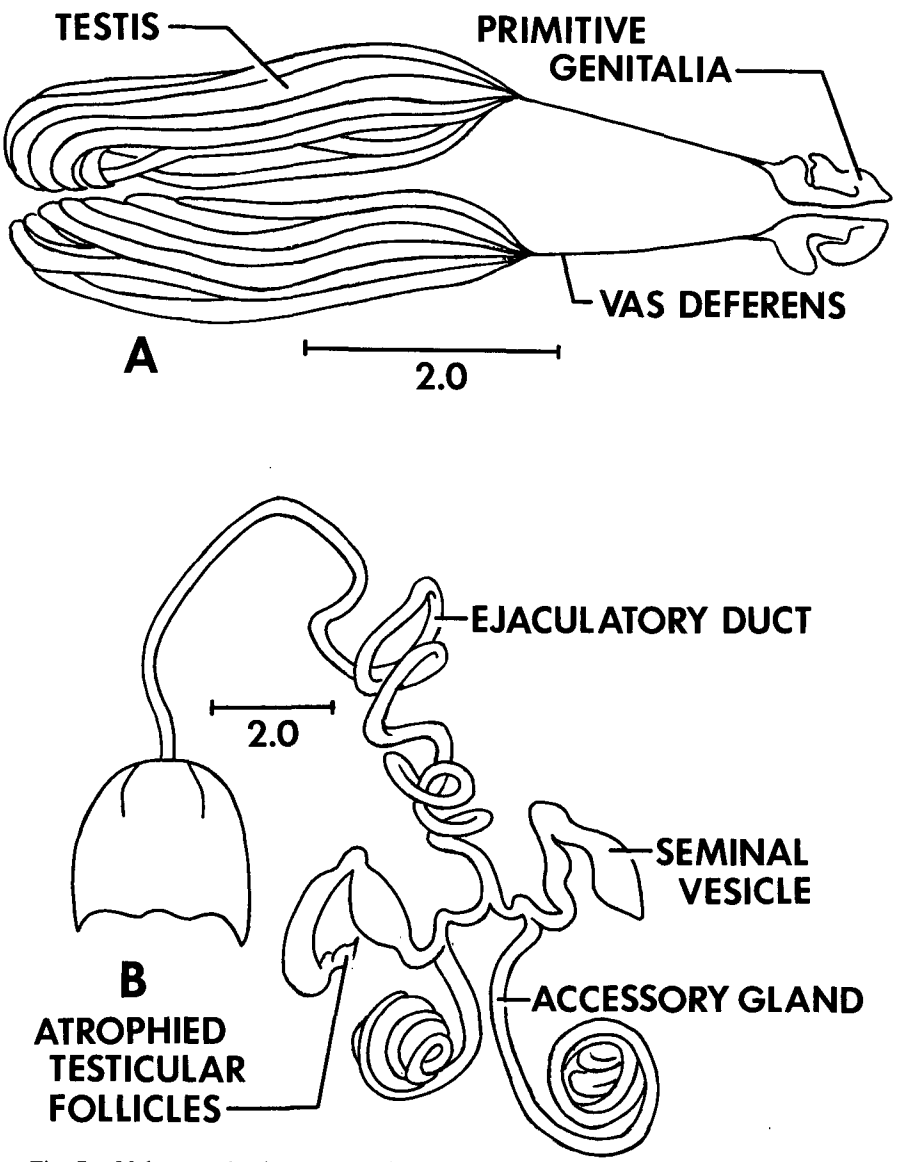


Fig. 7. Male reproductive system. A, *Neivamyrmex texanus* pupa, dorsal view. B, *Nomamyrmex esenbecki wilsoni*, structures displaced for purpose of display, dorsal view. Scales in mm.

longer than those of *Cheliomyrmex*. Although they are coiled, they do not wrap about the seminal vesicles. The ejaculatory duct loops ventrally before entering the genital capsule.

Serial sections of *Labidus coecus* (Latreille) reveal the presence of

"clumps" of sperm cells in the seminal vesicles. Each clump appears as a discrete unit of closely packed spermatozoa. The seminal vesicles are thin-walled sacs. The accessory glands are lined with a columnar epithelium that is unevenly distributed about the lumen of each gland. The epithelium is placed at opposite sides of the lumen, giving a bilateral organization to each gland (Fig. 4). Sperm cells were not present in the lumina of the accessory glands. Two lumina are present in the thick-walled ejaculatory duct and each is lined with an epithelium that stains the same color as the accessory gland epithelium. This epithelium is thickest on the median septum that separates the lumina (Fig. 5).

Neivamyrmex sp. (2 specimens from Pima County, Arizona) (Fig. 6). *Neivamyrmex nigrescens* (Cresson) (1 pupal specimen from Bell County, Texas) (Fig. 7A). *Neivamyrmex texanus* Watkins (1 pupal specimen from Waco, Texas).

Testes in the adult are not present. The seminal vesicles are large bulbous structures, each of which is bent back upon itself and enclosed in a membrane. Attached to the apex of each vesicle is a series of thin, tubule-like structures that may be the testes in atrophied form. Microscopically, these "tubules" reveal little except that they are not muscle fibers. A portion of the seminal vesicle, after being macerated, was examined under the compound microscope. This spongy tissue within each vesicle is composed of a compact mass of spermatozoa. The accessory glands are tightly coiled tubes lying on either side of the midsagittal plane next to the anterior end of the genital capsule. The seminal vesicles join the proximal ends of the accessory glands just before these glands unite to form the ejaculatory duct. This duct, containing two lumina, forms a ventrally directed loop that caudally enters the genital capsule.

Testes were prominent in both pupae dissected. The *N. nigrescens* pupa was still larviform with testes that extended the length of abdominal segments 4–6. Each pupal testis is composed of many elongated or tubular follicles (Fig. 7A), and each is connected, albeit tenuously, to the primitive genitalia by a rudimentary vas deferens.

Nomamyrmex esenbecki wilsoni (Santschi) (1 specimen from Rio Corona, Tamaulipas, Mexico (Fig. 7B).

A small group of atrophied testicular follicles attached to the distal end of one seminal vesicle. No other evidence of testes could be found. The seminal vesicles are flattened structures that fold back upon themselves once. They are similar to those of *Neivamyrmex* but not as bulbous. The accessory glands are tightly coiled, elongated tubes and are joined at their bases by the seminal vesicles. The ejaculatory duct is uniquely developed into a long tube that wraps around the ventriculus of the alimentary canal before looping ventrally and posteriorly. It then enters the genital capsule.

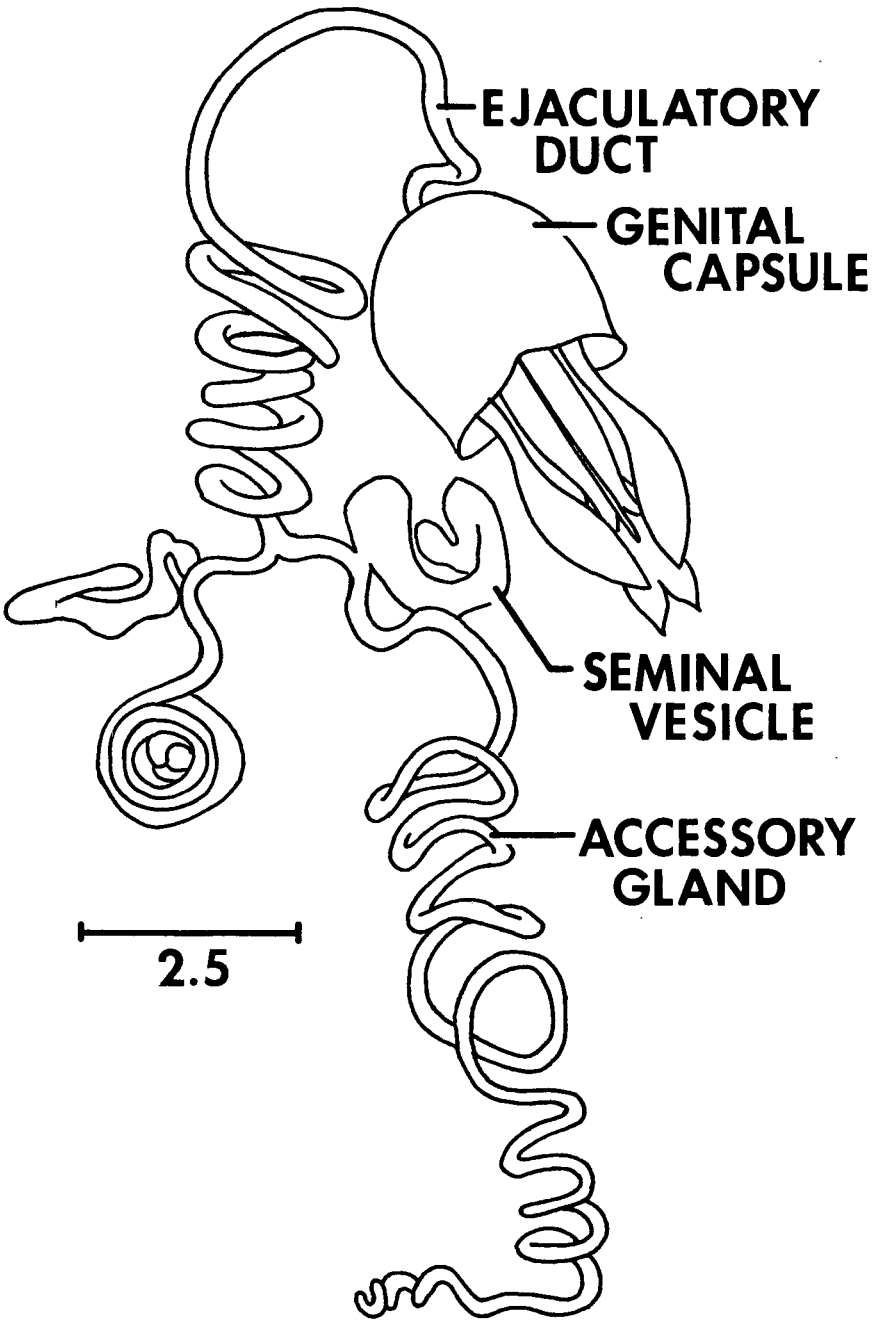


Fig. 8. Male reproductive system of *Eciton hamatum*, dorsal view, left accessory gland uncoiled. Scale in mm.

Eciton hamatum (Fabricius) (3 specimens from Barro Colorado Island, Panama Canal Zone) (Fig. 8).

Testes are absent. The seminal vesicles are flattened dorsoventrally and each is enclosed in a membranous capsule. Each joins its corresponding accessory gland near the proximal end of the gland. The accessory glands are long, coiled tubes. These glands lie on either side of the midsagittal plane juxtaposed to the anterior end of the genital capsule. The ducts from the accessory glands join to form a long ejaculatory duct that coils around the ventriculus of the alimentary canal. The lumina of the two ducts remain distinct throughout the length of this tube. The ejaculatory duct encircles the ventriculus in an anterior direction. At one point, it folds back upon itself, continuing around the ventriculus in the opposite direction but still proceeding anteriorly. Following the last coil, the duct loops back ventrally, i.e., beneath the ventriculus toward the posterior end of the gaster where it enters the genital capsule.

Subfamily Dorylinae

Aenictus sp. (2 specimens from Lamto, Ivory Coast) (Fig. 9A, B).

Although the seminal vesicles are encapsulated by a single membrane (Fig. 9A), testes are not evident within the membrane capsule. The seminal vesicles are elongated, convoluted structures (Fig. 9B). The accessory glands are short and closely applied to the anterior end of the genital capsule. These glands empty into a short ejaculatory duct that directly enters the genital capsule.

Dorylus (*Alaopone*) sp. (3 specimens from Kade, Ghana) (Fig. 9C). *Dorylus* (*Anomma*) sp. (3 specimens from Lamto, Ivory Coast) (Figs. 10A, 13, 14). *Dorylus* (*Anomma*) *nigricans* complex (3 pupal specimens from Rwantonde and Musasu, Rwanda) (Figs. 11, 12). *Dorylus* (*Dichthadia*) *laevigatus* (F. Smith) (2 specimens, 1 from Sandakan, Borneo, 1 with undecipherable locality label). *Dorylus* (*Dorylus*) sp. (2 specimens from Kibos near Lake Victoria, Kenya) (Fig. 15 A, B). *Dorylus* (*Dorylus*) sp. (2 pupal specimens from Rwantonde and Rubona, Rwanda) (Fig. 15C–E). *Dorylus* (*Typhlopone*) spp. (2 specimens from Kibos, Kenya; 1 from Kade, Ghana) (Fig. 16).

The morphology of the male internal reproductive system of *Dorylus* is relatively uniform throughout the subgenera. Only *Dichthadia* remains to be thoroughly examined. The two dried pinned specimens available for dissection did not, when treated, soften sufficiently, and the internal genitalic structures remained withered and rather amorphous.

Testes are not present in the adult male. In the pupae of *Dorylus* (*sensu stricto*) and *Anomma* they are massive structures, equal to or larger than

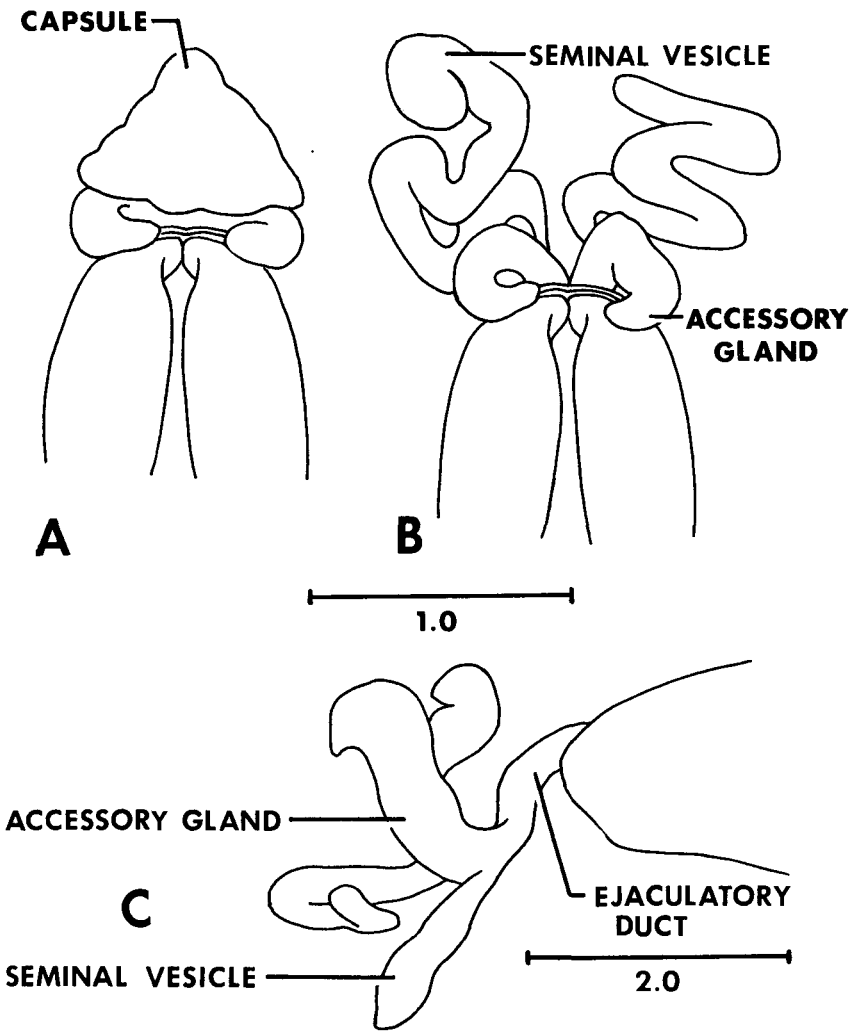


Fig. 9. Male reproductive system. A, *Aenictus* sp., *in situ*, dorsal view. B, *Aenictus* sp., capsule removed, dorsal view. C, Subgenus *Alaopone* sp., lateral view. Scales in mm.

the genital capsule of each individual specimen from which they were dissected. Each testis consists of many follicles, all of which converge upon and empty into the narrow distal end of the seminal vesicle (Fig. 15). Histologically, each follicle is predictably composed of spermatocysts consisting of small clusters of spermatogenic cells. Each spermatocyst is surrounded by a capsule of somatic cells (Figs. 11, 12). Pupae of the other four

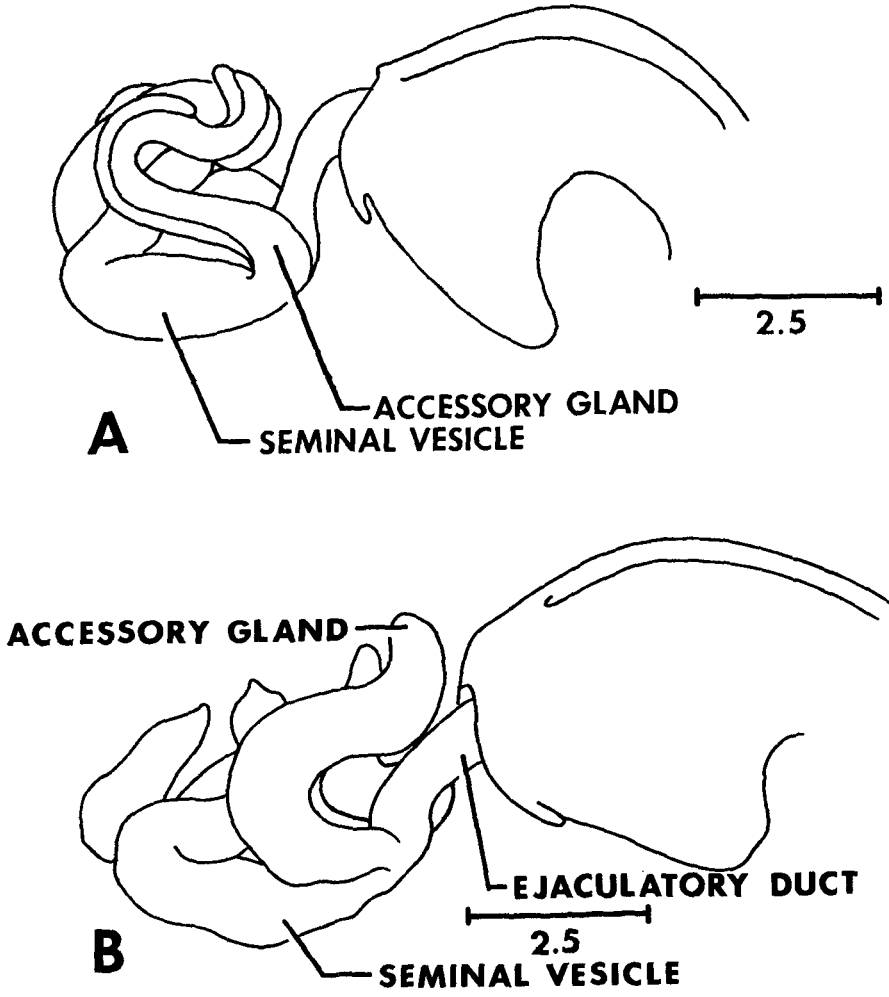
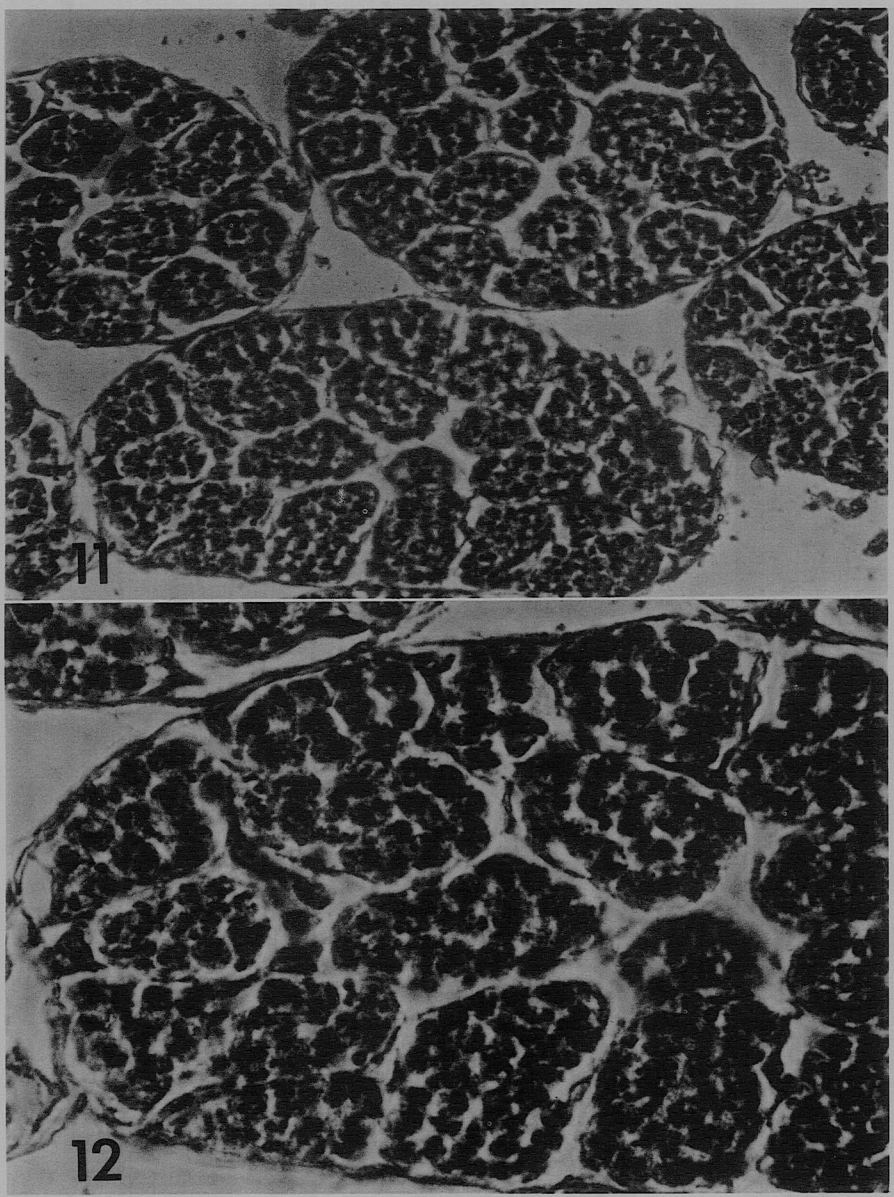


Fig. 10. Male reproductive system. A, Subgenus *Anomma* sp., outer covering of left accessory gland removed, lateral view. B, Subgenus *Rhogmus* sp., lateral view. Scales in mm.

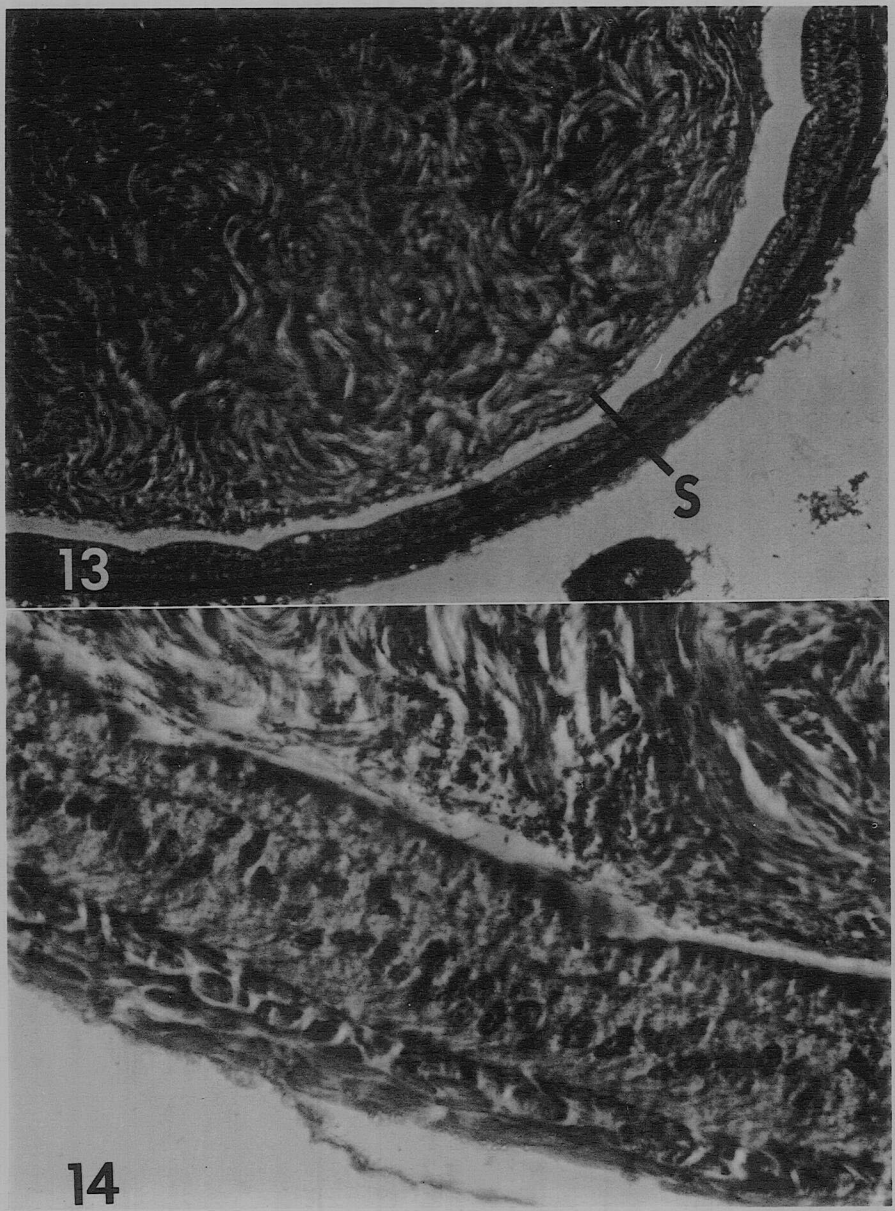
subgenera were not available for dissection, but there is no reason at the moment to assume that they differ significantly from *Dorylus* and *Anomma*.

The vasa deferentia are enlarged to form saclike seminal vesicles. These are elbowed, with their apices directed dorsally or posteriorly (Figs. 9, 10, 15, 16). They lay ventral to the accessory glands, which they superficially resemble, and they join the accessory glands ventrally at the proximal end of the glands. The wall of the seminal vesicle, at least in *Anomma* and *Rhogmus*, consists of a thin outer layer of muscle (?) and connective tissue and an inner layer, lining the lumen, of columnar epithelium (Figs. 13, 14).



Figs. 11, 12. Testis of pupa of *Dorylus* (*Anomma*) *nigricans*, cross section. 11, Several follicles (200×). 12, Single follicle with clearly defined spermatocysts (400×).

In *Rhogmus*, the lining is of uneven thickness in some places and in other locations is produced into a series of ridges. The lumen of the vesicle is filled with tightly packed spermatozoa.



Figs. 13, 14. Seminal vesicle of subgenus *Anomma* sp. male, cross section. 13, Portion of vesicle showing spermatozoa (S) in lumen (100×). 14, Detail of vesicle wall (400×).

The accessory glands appear saclike and usually curve or bend back upon themselves so that the distal half of each gland is directed dorsally or posteriorly (Figs. 10, 15, 16). *Alaopone* is the only exception to this general

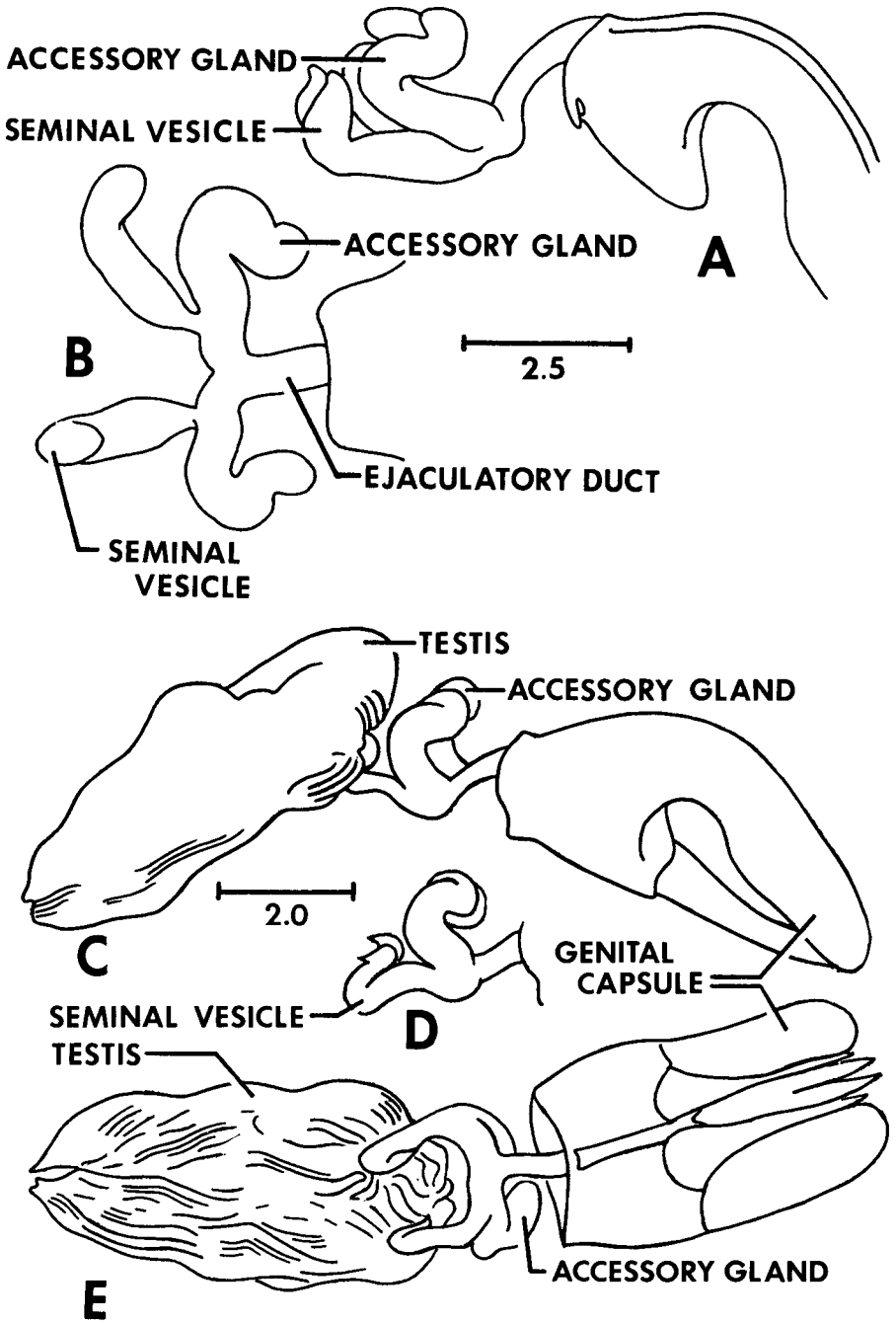


Fig. 15. Male reproductive system of subgenus *Dorylus* spp. A, Adult structures, lateral view. B, Adult structures, dorsal view. C, Pupal structures, lateral view. D, Internal pupal structures with testes removed, lateral view. E, Pupal structures, ventral view. Scales in mm.

morphology (see Fig. 9C). Removal of the outer wall reveals an internal, linear, hardened structure of unclear definition. Microscopically, in *Anomma* and *Rhogmus*, the wall of the gland is composed of two layers, an outer, probably muscular, layer and an inner layer of columnar epithelium. The outer layer is further subdivided into an outer coat of longitudinally arranged fibers and an inner coat of circularly arranged fibers. A lumen is present but its cross sectional shape is irregular because the lining is thrown into a series of ridges. These may represent the linear structures detected in gross dissection. The lumina of the glands sectioned were empty, except for the presence of some spermatozoa in limited areas in the *Rhogmus* specimen.

The ejaculatory duct is organized bilaterally with two lumina present. The epithelial lining is enlarged on the median wall in each lumen.

Discussion

It is not uncommon among male holometabolous insects for the testes to reach their greatest development in the pupa. In the honey bee, for example, spermatogenesis is already completed by the fifth or sixth day of the pupal period (Snodgrass, 1956). After emergence, the testes of the drone shrink and eventually, in about 12 days, they are reduced by more than two-thirds their maximum pupal length. Shrinking or atrophy of the testes following pupal eclosion is not quantitatively uniform throughout the ants, although information in the literature on this phenomenon is largely nonexistent. For instance, in *Myrmica rubra* Linnaeus, the testes are well developed and conspicuous (Janet, 1902) and quite evident as well in the ponerines *Rhytidoponera metallica* F. Smith (Hagopian, 1963) and *Plectroctena lygaria*. However, Hung and Vinson (1975) noted, in dissections of male pupae and adults of different ages from several ant subfamilies, that as the males mature, the spermatozoa descend into the vasa deferentia and the testes become progressively smaller. Marcus (1953) avoided altogether figuring the testes in several ant species without explanation. From our observations, we must conclude that the disappearance of the testes in the adult male army ant is a universal phenomenon in both the Ecitoninae and Dorylinae. Only in the dissected specimens of *Neivamyrmex* and *Nomamyrmex* was there any evidence of atrophied testicular follicles. While the crudeness of gross dissection technique might obscure the observation of such follicles, we submit that this is unlikely since we specifically searched for the structures. Certainly we found nothing like the prominent testes described pre-

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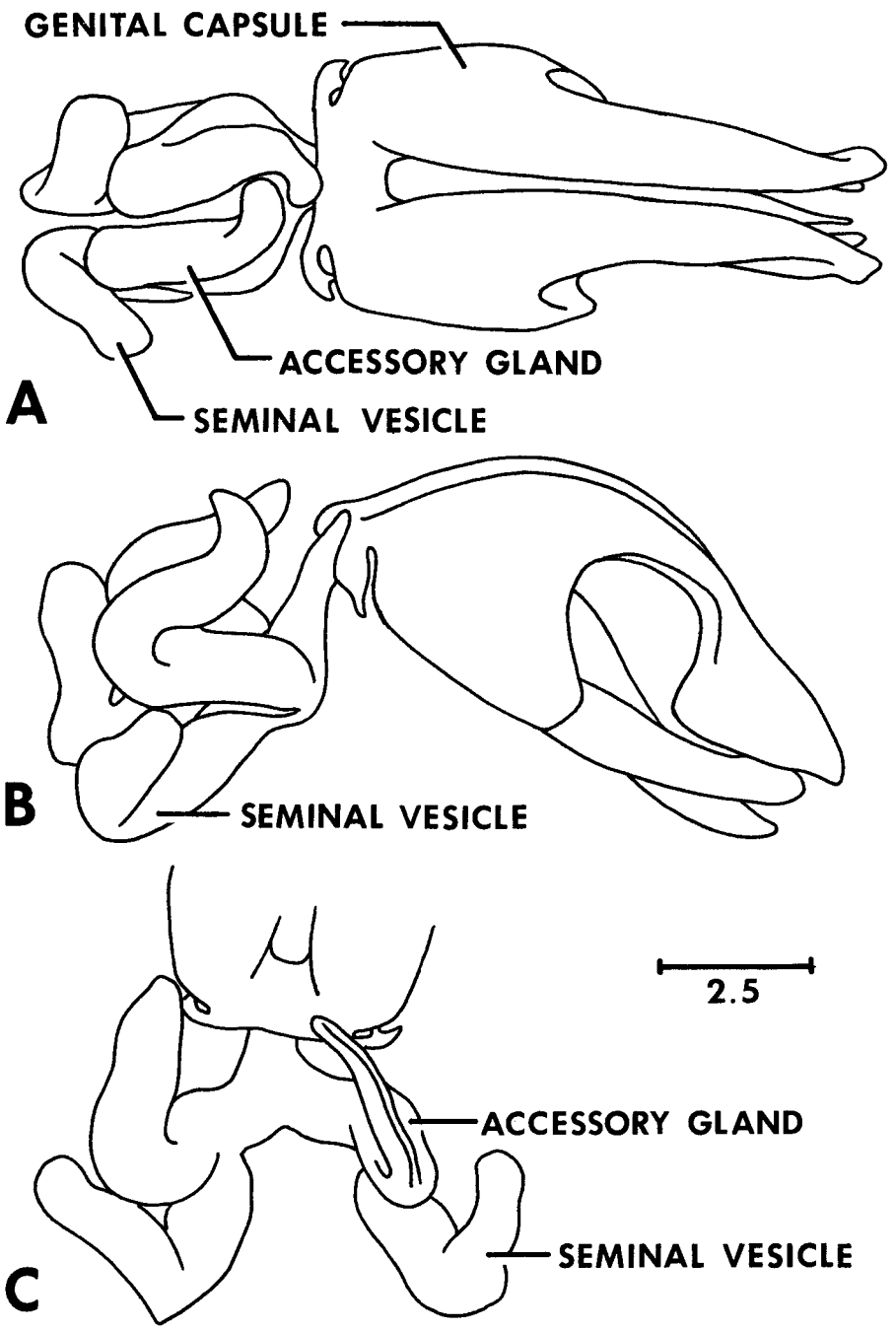
Fig. 16. Male reproductive system of *Dorylus* (*Typhlopone*) sp. A, Dorsal view. B, Lateral view. C, Internal structures displaced for purpose of display, outer covering of left accessory gland removed, dorsal view. Scale in mm.


GENITAL CAPSULE
ACCESSORY GLAND
A
SEMINAL VESICLE
B
SEMINAL VESICLE
2.5
ACCESSORY GLAND
SEMINAL VESICLE
C

viously for *E. hamatum* (Forbes, 1958) and *N. harrisi* (Forbes and Do-Van-Quy, 1965). Even so, the testes described and figured for those two species appear much smaller than we would estimate their size to be in the pupa. The *N. harrisi* specimens were collected on their "nuptial" flight and might have been rather newly emerged.

While the vasa deferentia of many ant species—and other Hymenoptera, for that matter (see Matsuda, 1976)—are slender tubes (Fig. 1), those of army ants are characteristically expanded to form seminal vesicles. Some confusion regarding these expansive tubes exists in the literature. For example, the term "seminal vesicle" has been incorrectly applied to the accessory glands in several instances (Forbes, 1954; Hagopian, 1963; Hung and Vinson, 1975). Usually the seminal vesicle of army ants is of rather uniform diameter throughout its length. This was not true of one specimen of *Typhlopone* that we dissected, nor was it so for the specimens of *D. (Typhlopone) labiatus* examined by Mukerjee (1926). In these specimens each seminal vesicle included two prominent swellings separated by a constriction. These dilatations proved not to be discrete structures but rather areas containing compact masses of spermatozoa. There can be not doubt that the expanded vasa deferentia serve in the storage of gametes, since closely packed spermatozoa have been found there in *D. (T.) labiatus* (Mukerjee, 1926) and *Neivamyrmex* (Forbes and Do-Van-Quy, 1965) in previous research and in all genera and subgenera in the present study.

The army ant males are noteworthy in two respects when compared to other ants: (1) their testes rapidly degenerate once they become imagos; and (2) their vasa deferentia are expanded to form seminal vesicles. The genera *Eciton, Nomamyrmex,* and *Neivamyrmex* possess uniquely formed accessory glands, and *Eciton* and *Nomamyrmex* have a distinctly produced ejaculatory duct. In fact, thus far, similarly developed genitalia have not been found elsewhere amongst the ants. The internal male genitalia of the New World army ants are conspicuously different from those of the Old World species.

Within the New World species, *Eciton* and *Nomamyrmex* are most derived, with their long coiled accessory glands and ejaculatory duct. *Neivamyrmex* lacks the coiled ejaculatory duct and has instead one that forms a ventrally directed loop. Certainly *Cheliomyrmex* and *Labidus* are least derived. Their accessory glands, while partially coiled, are short and more closely approximate in size those of other ants. This condition in the males is consistent with the primitive nature of these two genera, especially *Cheliomyrmex* in which the workers possess a uninodal waist (the waist is binodal in the workers of all other New World ecitonines). In the Old World species, most especially in *Dorylus,* the internal male genitalia are uniformly developed. Even *Aenictus,* a genus hypothesized to have arisen independently in tropical Laurasia in the early Tertiary (Gotwald, 1977, 1979), con-

forms closely to the general pattern, except in the containment of its seminal vesicles in a single membranous capsule.

Phylogenetic Conclusions

1. The male internal reproductive system of army ants is most derived in New World genera, especially in *Eciton, Nomamyrmex,* and *Neivamyrmex,* and least so in the Old World genera.
2. Morphology of the system within the New World species confirms the primitive nature of *Cheliomyrmex* and the generally derived state of *Eciton* and *Neivamyrmex.*
3. The system is uniform in the six subgenera of *Dorylus,* emphasizing the probable shared ancestry for these species.
4. Although the morphologies of the male system clearly reveal a dichotomy in development, supporting a diphyletic hypothesis of doryline origins (New vs. Old World species), they do not demonstrate a conspicuous difference between *Dorylus* and *Aenictus.*

Acknowledgments

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